Changes in adult Chinook salmon (*Oncorhynchus tshawytscha)* survival within the lower Columbia River amid increasing pinniped abundance

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Abstract

Significant effort towards conservation has contributed to the recovery of historically depleted pinniped populations world-wide. However, in several locations where pinnipeds have increased, they have been blamed for preventing the recovery of commercially valuable fish species through predation. Prompted by increasing pinniped abundance within the Columbia River (CR) USA, over a six year period, we used Passive Integrated Transponder tags to measure the survival of adult spring-run Chinook salmon (*Oncorhynchus tshawytscha*) through the estuary and lower CR to Bonneville Dam (Rkm 234). We estimated 51 751 - 224 705 salmon died annually from sources other than harvest. Mixed-effects logistic regression modelling identified pinniped predation as the most likely source. The odds of survival was estimated to decrease by 32% (95% CI: 6%-51% decrease) for every additional 467 sea lions, and to increase by 32% (95% CI: 8%-61% increase) for every increase of 1.5 in the log of American shad (*Alosa sapidissima*), a potential prey item for sea lions. A third covariate was the adipose clip status of the fish, indicating whether it was eligible for harvest.

Introduction

Recovery trends for historically depleted pinnipeds (true seals and eared seals) are reported to be moving in a positive trajectory for fifty percent of the world's populations (Magera et al. 2013). This is compared to 42% for marine mammals overall and 31% for cetaceans. Pinniped recoveries have been attributed to a combination of factors, including management and conservation efforts and life history traits such as their relatively fast life cycle (compared to cetaceans) and their tendency to breed and rear pups in remote but nearshore habitats (Magera et al. 2013). Recovery of eared seals has been particularly successful with 58% of the world's sea lion populations showing a significant increasing trend. In contrast, in several locations where pinnipeds have increased, depressed or depleted commercially valuable fish species have continued to struggle despite similar efforts towards recovery. Warranted or not, in many cases this has led to the gregarious and highly visible pinnipeds being blamed for concurrent fisheries recovery failures (Bombau and Szteren 2017; Ocampo-Reinaldo et al. 2016; Swain and Benoit 2015; Swain et al. 2015; Trzcinski et al. 2006). The U.S. Pacific Northwest offers no exception to this scenario. Since the 1980s pinnipeds have been accused of negatively impacting the recovery of protected Puget Sound and Columbia River (CR) steelhead and salmon runs. (Fraker and Mate 1999; Jeffries and Scordino 1997; Laake et al. 2018; Wright 2010). This manuscript describes a five year field study designed to determine the impact of increasing pinniped abundance on the survival of adult spring-run Chinook salmon (*Oncorhynchus tshawytscha*) returning to the Interior CR Basin. Importantly, our study illustrates methodology that goes beyond the theoretical food web modelling most often used to investigate whether or not top predators such as pinnipeds are significantly impacting their prey populations (Benoit et al. 2011; Buren et al. 2014; Houle et al. 2016; Ocampo-Reinaldo et al 2016).

We focused on spring-run Chinook salmon originating from the Middle (MCR) and Upper (UCR) CR and spring/summer-run Chinook salmon from the Snake River (SR). Study fish are collectively referred to hereafter as Interior CR spring-run Chinook salmon. The UCR and SR components include culturally and economically important native fish populations that have been protected under the Endangered Species Act (ESA) by the U.S. Federal Government for greater than 15 years (NMFS 1999; 1992 respectively). Despite protection, the status of the UC and SR populations has not improved significantly and their future viability remains uncertain (Ford et al. 2015).

Interior CR spring-run Chinook salmon possess a geographically diverse four to five year life cycle. Juveniles spend a year rearing in freshwater before migrating to sea during the spring of their second year, after which they spend an additional two to three years in the ocean growing and maturing. Mature adults return to the CR estuary in the spring with the peak return typically occurring during mid-May. Upon their return to freshwater they embark on an extensive (i.e. several hundred km) migration back to their natal tributaries and streams where they hold until late summer, spawn, and die (NOAA 2017; UCSRB 2007).

Given their varied life history, a multitude of factors are thought to have contributed to the decline of Interior CR stocks, including excessive harvest, alteration, degradation, and loss of freshwater habitat, and excessive hatchery production that competed with and threatened the genetic integrity of some natural populations (Myers et al. 1998; Chapman et al. 1991). However, to date, the majority of the information that we have about Interior CR populations has come from studies conducted on juvenile life stages (e.g. Smith et al. 2002, Scheuerell et al. 2009, Tomaro et al. 2012, and Miller et al. 2014). Aside from harvest related mortality, relatively little is known about the survival and behavior of Chinook salmon adults upon their return to freshwater.

After over 40 years of federal protection under the Marine Mammal Protection Act of 1972 (MMPA; 16 United States Code §1361 et seq.), the remarkable recovery of west coast pinnipeds may be detrimentally influencing the recovery of Interior CR Basin spring-run Chinook salmon through predation. West coast pinnipeds include the Oregon/Washington coastal stock of Pacific harbor seals (*Phoca vitulina*), the U.S. stock of California sea lions (*Zalophus californianus*), and the eastern stock of Steller sea lions (*Eumatopias jubatus*); all are potential predators of adult salmon. Harbor seals are present within the lower CR throughout the year and adult and sub-adult California and Stellar sea lions are present in significant numbers within the lower river from August through May (ODFW, unpublished data). Importantly, the peak pinniped presence within the river coincides with the adult spring-run Chinook salmon return migration.

Although it is evident that marine mammal predators of salmon have increased considerably along the northwest United States coast since the early 1970's (Barlow et al. 1995; Carretta et al. 2014; Laake et al. 2018; NMFS 1997) the exact number of pinnipeds by species that either enter intermittently or permanently reside within the CR annually is unknown. The Oregon and Washington Departments of Fisheries and Wildlife (ODFW and WDFW respectively) have conducted aerial surveys of harbor seals along their coasts and within their estuaries since 1977 (Brown et al. 2005). The information collected during the ODFW and WDFW aerial surveys serves as our best evidence the CR harbor seal population has increased along with the general population. For example, the number of non-pups observed at haul out sites within the CR based on aerial surveys conducted from 1995-2004, ranged from 250 to just over 1 000 animals on a given sampling day. In comparison, during 2005-2014 the number of animals observed on each survey day was consistently greater than 1 250 and on February 11, 2015, 6 422 harbor seals were observed at one location. The maximum daily number of animals observed prior to this date had been 2 200 (Jeffries et al. 2015).

ODFW has been trapping and branding California sea lions at the East Mooring Basin in Astoria, Oregon since 1997 (Wright et al. 2010 & Elorriaga-Verplancken et al. 2014). Additionally, they have been counting the number of individual sea lions (*Zalophus & Eumatopias)* utilizing this location as a haul out site during the spring on a weekly basis. The information collected for this study is the best indicator of sea lion abundance within the river. Although the number of sea lions entering the river each spring was consistent from the late 1990s through 2012, there have been recent notable increases. For example, during 2010-2012 (as well as during the decade prior), the median number of individuals observed (Zalophus and Eumetopias combined) on a single day between May 15 - 31 ranged from 126-137 and peak daily counts ranged from 250-350 individuals. In comparison, during 2013, the median number of animals observed during the last two weeks of May was 450 and the most animals observed at the East Mooring Basin during a single day increased to 750. During 2014 and 2015, the median number of sea lions observed during the last two weeks of May was 375 and 576 respectively, and peak daily counts reached 1 350 and 2 340. Sea lions entering the CR are nearly exclusively comprised of adult and sub adult males (Wright et al. 2010).

Biologists have been estimating Chinook salmon consumption within the quarter mile reach below Bonneville Dam (Rkm 234) since 2002 (Stansell 2004 and Tidwell et al. 2017). Estimates of predation in the vicinity of the dam have ranged from a low of 0.3% of the annual Interior CR spring-run Chinook salmon return in 2002 to a high of 4.3% in 2015 despite a history of active harassment, relocation, and the lethal removal of predators at this location (Tidwell et al. 2017). Bonneville Dam is the most downstream hydropower dam in operation on the mainstem CR and with very few exceptions this structure serves as a physical barrier to the upstream movement of pinnipeds. Notably, less than 10% of the sea lion population entering the river each year and virtually no harbor seals venture as far upriver as Bonneville Dam (ODFW, unpublished data; Tidwell et al. 2017). Therefore, the majority of the predation that has occurred within the CR has likely been unaccounted for.

Our study is the first to provide estimates of salmon survival through the entire freshwater reach below Bonneville Dam in an effort to better understand the magnitude and timing of non-harvest related mortality for returning CR adult salmon. Despite extensive efforts to supplement natural spawning populations through artificial propagation and the captive rearing of wild broodstock, recovery goals for natural origin UCR and SR spring-run Chinook salmon spawners are not being met (ODFW and WDFW 2016; NOAA 2017; UCSRB 2007). We hypothesized that predation of adult salmon through the estuary and the freshwater reach below Bonneville Dam was significantly higher than what was being observed and recorded within the quarter mile reach below Bonneville Dam and that it was having a significant negative impact on the viability of Interior CR spring-run Chinook salmon populations.

Materials and methods

During spring 2010-2015 we collected both hatchery (adipose fin-clipped to denote artificially propagation) and presumed wild (adipose fin intact) adult Chinook salmon on multiple dates from the CR estuary east of Astoria, Oregon near River km 44 (Fig. 1; Table 1). We worked with experienced commercial fishermen who used tangle-net fishing gear (4.25 inch stretch mesh) designed to ensnare adult salmon by their teeth rather than closing in around their gills which can lead to death through suffocation. A typical commercial tangle-net is approximately 275 meters in length and extends to a depth of approximately 12 meters. Soak time or set durations during our sampling ranged from 25-40 minutes. Shorter soak times were employed as water temperatures increased and if pinnipeds were present within the sampling area. We actively discouraged pinnipeds from entering the sampling area through use of cracker shells and seal bombs, harassment devices permitted in the commercial fishery.

Individual salmon were taken from the nets and placed into customized plastic tubes designed for fish handling. Fish tubes were hung over the side of the vessel to keep fish within the river. They were then transported from the sample boat to a tagging vessel where they were placed (still within their tube) into a 2,839 liter holding tank with flow-through river water until they could be tagged (Fig. 2a). On average, we rejected 3% (1% -5% annually) of landed fish for tagging due to mortality or severe injury (primarily by predators) during sampling.

Study fish were restrained in ventral recumbency using a custom aluminum fish handling device (Figs. 2b and 2c). This device allowed us to measure, tag, and collect tissue samples (i.e. fin clips) from study fish without removing them from the water and without using anesthesia. Treatment fish were also scanned for a pre-existing Passive Integrated Transponder (PIT) tag prior to tagging. Previously PIT-tagged fish were included in the study without subjecting them to further handling. Untagged fish were injected subcutaneously in the region of the pelvic girdle with a 12-mm PIT tag (2.0 mm diameter; 0.1 g in air). The length of time required to process and tag each fish was typically less than 90 seconds. Tagged fish were then held in tubes for a minimum of five minutes before they were released back to the river to resume their migration (Fig. 2d).

Fin tissue clipped from tagged fish was stored in 70% ethanol for genotyping. During 2010-2013 genetic stock identification analyses was conducted in the manner of Teel et al. (2009). Fin tissues from tagged fish were genotyped for a set of 13 microsatellite DNA loci from a standardized database developed by nine West Coast salmon genetics laboratories (Seeb et al. 2007, Hess et al. 2014). We used the genetic stock identification program ONCOR (Kalinowski et al. 2007) to identify the stock origins of individual fish. For the survival analyses in our study, we assigned fish to one of two groups: fish originating above Bonneville Dam (Interior CR spring-run) and below the dam. Only tagged salmon identified to have originated from tributaries above Bonneville Dam were included in the survival analyses. To improve assignment accuracy only fish with relative probability assignments of 0.95 or greater were used. Individual fish were then assigned to one of nine potential genetic stock identification groups for the CR basin (Seeb et al. 2007; Teel et al. 2009). During 2014, in place of the microsatellite loci, we began using 192 single nucleotide polymorphism (SNP) loci to identify the genetic stock of origin (Ackerman et al. 2015).

In most years, sampling commenced on or before April 1 and proceeded through mid- to late May for a maximum of 12 weeks per year (Table 1). With the exception of 2010 and 2013, we initiated sampling based on catches from a local test fishery that indicated we could reliably land at least six fish daily. Initiation of sampling in 2010 and 2013 was delayed due to us receiving late funding for the study. Therefore, the early arriving spring-run Chinook salmon were not represented during 2010 and 2013 (Fig. 3). Our sampling season concluded when our mean daily catches were less than six fish.

From 2010 through 2015 we implanted (or detected) PIT-tags into 2 106 Chinook salmon as they returned to the CR estuary from the ocean. Of our tagged fish, 1424 were identified as belonging to our target study group, i.e. adults (defined as age ≥4 years based on having a FL ≥ 560 mm) originating from tributaries above Bonneville Dam with greater than 0.95 assignment probability, and released during the same week as at least four other fish. Forty-eight percent of our target study group was identified as being from the UCR and MCR and 52% as being from the SR. This compares to estimates of 44% and 56% from the UCR, MCR and SR respectively for the run at large during 2010 – 2015 (ODFW and WDFW 2016). Twenty-four percent of tagged fish were presumed to be of natural origin due to having an intact adipose fin (UCR and MCR; 25%, SR; 22%). The median fork length of tagged fish was 750 mm and the range was 560 mm – 990 mm. Fork length was similar for fish originating from the UCR, MCR and SR.

Once the annual adult spring-run Chinook salmon migration past Bonneville Dam was complete, we queried the PTAGIS database (www.ptagis.org) for detections of our study fish within the CR hydro-system. PTAGIS is a regional database administered by the Pacific States Marine Fisheries Commission that houses tagging and detection information about PIT-tagged CR fish. etection records from our study fish detected at PIT-tag arrays in the adult ladders of

Bonneville Dam or at locations above were used to determine if fish survived from the release location to Bonneville Dam. Detection of adult salmon at Bonneville Dam during the spring migration was expected to approach 100% based on an earlier study of detection efficiency conducted at this site (Burke et al. 2006).

Logistic Regression Analyses

We applied a generalized linear mixed-effects model (GLMM) to the data indicating individual fish survival to Bonneville Dam. We considered tagged fish to have survived if they were detected at or above Bonneville Dam. Fish not detected at or above Bonneville Dam were presumed to have died within the lower river. GLMM modeling extends regression by allowing for both fixed and random effects to account for variation in measured response variables (Hosmer and Lemshow 2013). We included a random effects component where weekly effects were nested within annual-level variation, and also followed an autoregressive order-1 (AR1) covariance structure. This random effects structure followed naturally from the hierarchical way in which the data were collected and organized, and allowed survival among proximal release groups to be similar in ways beyond that captured by the covariates. To ensure that our parameter estimates were not biased by small sample sizes, we excluded any release weeks with less than five fish tagged and released. Weeks were defined in our model as the number of full weeks (Sunday-Saturday) since January 1st of every year.

In addition to the weekly random effect, we included four fixed effects covariates in the fully parameterized logistic regression model (Table 2). We included length as a covariate based pinniped diet studies indicating smaller prey (i.e. < 30 cm length) are preferred (Adams 2016; Etnier and Fowler 2005; Thomas 2017) and based on our own hypothesis that larger fish may be stronger and thus more able to avoid predators during their migration to Bonneville Dam. We also included the adipose clip status of each study fish (i.e. whether or not they were legally eligible for removal through recreational and commercial harvest) because we hypothesized that mortality from harvest would be significant and higher for clipped fish compared to unclipped fish that if incidentally caught and landed alive are mandated to be released (ODFW and WDFW 2016; Fig. 4d).

We tested indices for American shad (*Alosa sapidissima*) abundance under the hypothesis that American shad provide an alternative prey source for pinnipeds, thus leading to higher salmon survival when both species are present (Hasselman et al. 2012). Similar to salmon, American shad are anadromous. Adults typically return to the CR from the ocean between May and July to spawn each year, overlapping the adult spring-run Chinook salmon return (Petersen et al. 2003). American shad have been identified as a top three prey item of pinnipeds within the quarter mile observation area below Bonneville Dam (Stansell 2011). Although a major component of American shad spawning occurs within the estuary and the lower CR, since the 1990s greater than 2 million American shad annually have also spawned at various locations above Bonneville dam (Petersen et al. 2003). Counts of returning adult shad over the dam currently serve as our best indicator of their abundance. For 2010 - 2015 we adjusted daily shad counts over Bonneville Dam back (i.e. earlier) two weeks to estimate American shad abundance within the estuary during the weeks our fish were tagged. Our decision to use a two week adjustment was based on rates of travel for American shad through an east coast estuary U.S.A. (Moser and Ross 1994). Due to the large range in the observed abundance of American shad, this covariate was log transformed. Figure 4b illustrates how American shad abundances changed through time.

The effect of predator abundance on salmon survival was tested using a covariate describing sea lion abundance because we hypothesized predation mortality through the freshwater reach below Bonneville Dam was significant and increasing. This hypothesis was based on increasing observed predation mortality within the quarter mile reach below Bonneville Dam for a subset of the CR pinniped population (Madson et al. 2016). This covariate is illustrated in Figure 4c and used the ODFW sea lion abundance estimates (*Zalophus & Eumatopias*) at the East Mooring Basin in Astoria, Oregon during the week a fish was released (ODFW, unpublished data)[1]. We also included an interaction between American shad abundance and sea lion abundance because anecdotal reports from CR commercial fishermen indicated that sea lions may feed preferentially on American shad, thus exhibiting prey-switching behavior.

Many of the additional variables we hypothesized might be influencing salmon survival were strongly correlated with covariates already described, so they were not included in our fully parameterized model. This included the abundance of Eulachon (*Thaleichthys pacificus*) in the river. Eulachon are anadromous smelt that return to lower CR tributaries as adults between December and April each year to spawn. Eulachon are preferred prey items of pinnipeds and over the course of our study eulachon biomass increased within the CR approximately 26-fold, peaking in 2014 (Gustafson et al. 2016). In our analysis, we found that

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[1] Fig. S1. Shows sea lion abundance at the East Mooring Basin, Astoria, Oregon on each Julian day throughout the survey period.

the annual abundance of eulachon was highly correlated (0.83) with the annual abundance of California Sea Lions in the CR estuary.

All continuous covariates were scaled by subtracting the mean and dividing by the standard deviation (Becker et al. 1988)[2]. The binomial response 'survival' was fitted using a logit link. Based on the above, our model GLMM for the survival (π) of adult salmon was:

$$logit\left(\pi_{w,i(j)}\right) = \boldsymbol{X}_{w,i}\beta + \alpha_{i(j)}; \alpha_{i(j)} \sim N\left(\mu_{i(j)}, \Sigma\right),$$

where *w* indexes individuals, *i* indexes weeks, *j* indexes years, ***X*** is a design matrix containing covariates values, β is vector of regression coefficients, μ is a vector of mean values whereby weekly random effects values are nested with years, and **Σ** is an AR(1) variance-covariance matrix with 1-unit lags defined on a weekly time scale.

The appropriate random effects covariance structure was not available, to our knowledge, in a readily available R package implementing maximum likelihood estimation, and given the complex random effects structure we expected long run times for our preferred Bayesian implementation. As such, we opted to proceed akin to Som et al. (2017), who when faced with a similar situation, first implemented a phase of maximum likelihood model selection under a similar random effects structure (to their target), and given the model selected from that phase, based all inference on estimates generated from a Bayesian implementation containing the fully appropriate random effects structure. In our case, candidate models were fit initially with the 'lme4' package in R (Bates et al. 2015), ranked using the Akaike information criterion (AIC; Burnham and Anderson 2002), and then the selected fixed effects covariates were fit with the nested AR1 random effects structure noted above

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[2] Fig. S2. Shows collinearity plot between all standardized covariates considered in the GLMM.

using JAGS (Plummer 2014). We included clip status in all potential models because of hypothesized increased harvest mortality of clipped fish. Thus, our model set consisted of ten models. From the candidate models, we selected the model with the fewest parameters and a delta AIC < 2.

For the Bayesian implementation of our final model, we specified generally non-informative priors. Mean-zero Gaussian priors with precision (variance^{-1}) values equaling 0.001 were selected for all regression coefficients and the means of the temporal random effects (weeks nested within years). For the AR(1) variance-covariance matrix associated with the temporal random effects, we specified a uniform prior over the positive support of the parameter space for the correlation parameter, (Ver Hoef and Jansen 2007), and a uniform (alpha, beta) prior (Gelman 2006) with alpha = 0 and beta = 10 (Ver Hoef and Jansen 2007) for the standard deviation parameter.

We ran three simultaneous Markov-Chain Monte Carlo (MCMC) chains and retained 3 000 samples per chain after a burn-in period of 100 000 samples and a thinning rate of 125 (i.e., 9 000 samples per parameter were summarized for inference). Convergence was assessed visually from traceplots of each MCMC chain, and quantitatively via Gelman-Rubin convergence statistic (Rhat) statistics (Gelman et al. 2014). Rhat values are calculated using the stability of outcomes between and within the MCMC chains of the same length, and values close to one indicate convergence to the underlying distribution.

The classification accuracy of the selected model across the range of our data was evaluated using area under the receiver operating curve implemented via the ‘pRoc’ package in R (Robin et al. 2011). This package plots the probability that a given model will identify both a true signal and a false signal correctly over a range of probability cutpoints and calculates the area under the resulting curve, known as the receiver operating characteristic (ROC) curve. The area under the ROC curve can range from between 0.0-1.0 and this is used as an indicator of a model's ability to discriminate between a true positive outcome (i.e. predict that a survivor will survive) and a true negative outcome (i.e. predict that a fish that died will die; Hosmer and Lemshow 2013). ROC values near 0.5 suggest poor discriminating tools with performance matching random classification, values below 0.5 (though uncommon) suggest that better discriminating outcomes would result by predicting the opposite of that suggested by the model, and values exceeding 0.5 indicate the model generally provides correct predictions between the two available options. We evaluated our ROC scores according to Swets (1988) where ROC values of at least 0.7 are considered predictors with good accuracy. Odds ratios for each of the covariates in the final model and their associated 95% confidence intervals were obtained by exponentiating their respective median regression coefficients and associated 95% credible interval.

Non-harvest mortality

Using our logistic regression, we estimated the amount of mortality not due to harvest (hereafter referred to as non-harvest mortality) during the upriver migration from the estuary to Bonneville Dam. Potential sources of non-harvest mortality include predation and delayed mortality due to sampling, handling, tagging, and disease. Upriver fish that strayed into lower river tributaries would have also appeared as mortalities given our study methods. The total number of fish that survived to Bonneville was estimated using counts at the dam. We then back calculated when the fish that survived to Bonneville were in the estuary (Ne) using a normal distribution mixture model based on the observed transit times. For weeks with no transit time data we estimated transit times based on the observed patterns (Fig. 4a). We used a linear regression for each year to estimate transit times prior to week 15 and assumed transit times after week 17 were equal to the mean of the final three observations. Finally, we sampled from the posterior distributions for the intercept, sea lion abundance, and American shad abundance 100 000 times to estimate a range of expected total mortality (Z). We did not sample from the clip parameter posterior because the unclipped fish had a much lower fishing mortality and were thus more representative of the non-harvest rate. We used the following equation to estimate the total number of fish that died due to natural causes (M) for each release week (i) in each year (j):

$$\boldsymbol{M_{i,j} = \left(\frac{Ne_{i,j}}{(1-Z_{i,j})} * Z_{i,j}\right) - c_{i,j},}$$

where c is the estimated number of unclipped fish harvested by the recreational, commercial, and tribal fisheries.

Results

Detection and survival-A total of 904 study fish were detected within the CR hydrosystem and of these study fish, 890 were first detected at Bonneville Dam. The 14 fish detected at locations above Bonneville Dam for the first time were detected during 2010 (N=3), 2011 (N=2), 2013 (N=1), 2014 (N=1), and 2015 (N=7). Figure 4e illustrates survival by release week and year for tagged fish[3].

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[3] Table S. 1. Shows the average daily survival by month across all years along with the average river temperature at tagging.

Travel time-The annual median travel time to Bonneville Dam (approximately 190 rkm from release) for survivors was 15, 22, 21, 13, 21 and 14 days respectively for 2010, 2011, 2012, 2013, 2014, and 2015. Each year of the study there was a consistent trend towards faster travel to Bonneville Dam for fish tagged progressively later in the season (Fig. 4a). Within year differences between individual fish sampled early compared to later in the run equated to 15, 28, 27, and 23 days respectively for 2011, 2012, 2014, and 2015. Travel times were similar for UCR and MCR (median= 21 d; range = 8-35 d) and SR stocks (median = 21 d; range = 5-57 d). Travel times were also similar for unclipped (median = 21; range = 5- 51 d) and adipose clipped fish (median = 21d; range = 5-57d).

Model selection and validation- After excluding weeks with less than five fish tagged and released, we had 1 424 individual fish tagged in 41 weeks with which to build our linear models (Table 1). Of the ten candidate GLMM survival models, two models had a delta AIC < 2 (Table 3). Of the two equivalent models, we selected the model with the fewest parameters because the additional parameters did not greatly improve the model fit. In addition to the random effect for release week nested within year (that was included in all models tested), our chosen model also included covariates describing sea lion abundance (California sea lion), the logged abundance of adult American shad within the lower CR, and whether or not fish had intact adipose fins (Clip) as fixed effects. The area under the receiver operating characteristic (ROC) curve from the Bayesian implementation was 0.70 (0.68-0.71 95% CI) indicating the final model was good with respect to discriminating salmon survival from mortality (Swets 1988).

Our model diagnostics indicated that we met all conditions necessary to make inferences from our posterior distributions. The Rhat values for each parameter were < 1.1, suggesting that all three MCMC chains converged to the same posterior space in all cases. Visually, the traceplots showed no indication that further burn-in, thinning, or additional posterior samples were necessary to proceed with inference.

Based on the posterior distribution estimates, and after accounting for weekly and annual variation unexplained by the fixed effects covariates, there was very strong evidence that each covariate retained in the inference model was related to salmon survival (Table 4). To quantify this effect for the continuous covariates we estimated the odds of survival with a one standard deviation increase in the covariate values (implicit from the standard center-and-scaling we applied to all continuous covariates), which was 467 sea lions and 1.5 for the log shad abundance (approximately 720 shad). Based on this model and the posterior distribution samples for our fixed effects parameters, the odds of survival for fish without adipose fins was estimated to be 34% lower (95% CI: 13% - 51% lower) compared to fish with adipose fins, the odds of survival was estimated to decrease by 32% (95% CI: 6% - 51% decrease) for every additional 467 sea lions, and for every increase of 1.5 in the log of American shad abundance the odds of survival was estimated to increase by 32% (95% CI: 8% - 61% increase). On the more easily interpretable scale of probability of survival, the biological significance of the effects of increasing sea lion and American Shad abundance, and whether or not fish had an adipose fin were apparent over the range of covariate values observed in this study (Fig. 5). Finally, there was evidence of temporal autocorrelation among the weekly-stratified observations (Table 4), and although the posterior distribution for the autocorrelation parameter was relatively diffuse, with only 41 individual weeks included in this study we would not have expected precise estimates for parameters of the variance-covariance matrix (Irvine et al. 2007).

***Non-harvest* –** We estimated that non-harvest mortality during the upriver migration from the estuary to Bonneville Dam varied considerably. For the years where we had the best temporal coverage of the run (i.e. 2011, 2012, 2014, and 2015) we estimated the number of fish that died during the upriver migration ranged from a low of 51 751 (95% CI 29 047 – 85 260) in 2012 to a high of 224 705 (95% CI 85 742 – 497 896) in 2015 (Table 5). During 2011 and 2012, the proportion of fish that died due to natural causes ranged from 0.20-0.22. In contrast, this proportion was 0.29 in 2014 and 0.44 in 2015.

Discussion

This study provides evidence that California sea lions entering the CR each spring are associated with reductions in the survival of adult spring-run Chinook salmon from the targeted populations. The most parsimonious model fit to survival data for PIT tagged adult Chinook salmon included parameters for California sea lion abundance, American shad abundance, and whether or not the fish had a clipped adipose fin and thus could be legally harvested. We hypothesize that the observed decreasing survival rate over this five-year period was due to increased predation pressure from the California sea lions, and other pinnipeds. Furthermore, our model indicated that adult salmon survival increased relative to American shad abundance. American shad are also a potential prey item for sea lions, thus, we hypothesize that larger abundances of American shad resulted in decreased predation pressure on adult salmon.

For at least a decade prior to this study, the abundance of sea lions within the CR during spring had been relatively consistent (ODFW, unpublished data). This consistency persisted into the early years of our study (i.e. 2010-2012) However, beginning in 2013, and just as the annual survival for our study fish began to decline, the number of sea lions (Zalophus and Eumetopias) entering the CR began to increase. Since the enactment of the MMPA, west coast pinniped populations have experienced significant growth and expansion (Laake et al. 2018). However, the sudden influx of animals into the CR during 2013-2015 after a period of relative stability was likely in response to changes in food availability rather than a species recovery response. The period of 2010 through 2016 saw the eastern Pacific Ocean at its warmest and least productive state in recent decades. (McClatchie et al 2016). It was characterized by an El Niño in 2010 (Bjorkstedt et al. 2011) and an oceanic heat wave (*i.e.*,The Blob) in 2013-2015 (Leising et al. 2015, McClatchie et al. 2016). These events caused major vertebrate assemblages of the California Current to be displaced geographically and affected prey availability for juveniles and pregnant and lactating female pinnipeds that remain within coastal California waters year round. In 2012 an unusual mortality event was declared for California sea lions due to unprecedented mortality of young of the year brought on by females' inability to maintain lactation sufficient to rear their pups (Melin et al 2012). There was simply inadequate prey available in the central and southern California Current within foraging range of adult females. Coincident with the warm surface waters and the lack of prey off central and southern California, an unusually large fraction of adult, subadult and even some juvenile male California sea lions moved north into Oregon and Washington waters in search of prey. Many of those found their way into the CR in the winter months of January, February, and March. This increase in sea lion abundance within the lower CR also corresponded with an increase in the biomass of Eulachon (*Thaleichthys pacificus*) in the river. Thus, we suspect that eulachon attracted predators into the CR. It may be that the future status and trends in the eulachon population will drive abundance of sea lions in the river in coming years. However, we may also observe that the increased pinniped presence will persist due to an abundance of animals having 'discovered' there is salmon available to them at this location.

Our estimates for the non-harvest mortality during the upriver migration were consistent with theoretical estimates of sea lion predation for the CR obtained through bioenergetics modelling. For example, we estimate 98 498 (57 200 - 158 520) Interior spring-run Chinook salmon adults died due to natural causes within the freshwater reach below Bonneville Dam during 2014 and 224 705 (85 742 – 497 896) died during 2015. In comparison, Chasco et al. (2017) used information about pinniped bioenergetics to estimate that during 2014 and 2015 respectively 119 000 (90 000-150 000) and 172 000 (131 000 – 218 000) total salmon (includes lower and upper river stocks) were predated upon by sea lions within the CR. The temporal trend in survival whereby fish tagged earlier in the spring had lower survival than those tagged latter was also consistent with patterns of predation observed by others. For example, Keefer et al. (2012) who studied pinniped predation of adult salmon directly below Bonneville Dam from 1996-2010 concluded that the highest proportional impact of predation was experienced by fish that returned to the dam during late winter and early spring compared to those that followed.

In attributing non-harvest related mortality estimates primarily to predation, we make the assumption that fish were not dying in the estuary or lower CR due to illness or due to the delayed effects of sampling and handling. We also assume fish were not straying into lower river tributaries and that harvest was not underestimated. Published information about the general health of adult spring-run Chinook salmon upon their return to the estuary is lacking. However, we did not observe outward evidence of disease in any study fish as might have been exemplified by pale gills or hemorrhagic gills, fins, or vent. Handling mortality for tangle net sampling has been determined to be 13% for CR Chinook salmon by the Technical Advisory Committee (TAC) to U. S. v Oregon (2008) based on the recommendation of Ashbrook et al. (2008)[4]. However, we believe that handling mortality during our study was less than this 13% criterion. This is primarily because several release groups tagged late in the season (i.e. during May and June) had 100% survival to Bonneville Dam when water temperatures were warmer and less ideal for sampling and handling. We also did not include fish that were lethargic upon release in our sample.

In a recent review study, Keefer and Caudill (2014) found the mean stray rate for CR *stream type* Chinook salmon (i.e. spring-run Chinook salmon such as our study fish) was consistently below 5%. Individual case studies where stray rates were higher than 5% were characterized by small sample sizes or a tendency for fish to stray locally (i.e. into nearby tributaries). Keefer and Caudill (2014) concluded stream type Chinook salmon from the CR that returned to streams other than their natal stream as adults tended to at least return to the region wherein they had originated. For example, fish originating from above Bonneville Dam strayed into tributaries above Bonneville Dam, fish that originated from the Willamette River

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[4] This estimate was held constant over the course of the study and did not include pre-landing mortality due to net suffocation or sea lion predation.

strayed into Willamette River tributaries, and lower CR fish strayed into lower CR tributaries. Behavior of our lower river study fish has remained consistent with this conclusion. To date, we have not observed a salmon identified as being from the lower river detected at or above Bonneville Dam. Similarly, to our knowledge, fish identified as being from upriver have not been detected in or collected from lower CR tributaries.

Harvest estimates for clipped and unclipped fish were provided by WDFW and ODFW and included sport and commercial catch below Bonneville Dam and landings from tribal hook and line fisheries below the dam (ODFW and WDFW 2016). Examination of the survival and harvest data indicated that the observed differences in survival between clipped and unclipped fish are accounted for by the reported differences in harvest for the two groups. However, if harvest is being underestimated for both clipped and unclipped fish, the estimates of non-harvest mortality reported here would be biased high. There is currently no reason to believe that harvest is being underreported. However, there may be a small component of predation that is related to harvest through depredation from fishing gear. Anecdotal reports from fishermen of this phenomenon have increased in the CR along with increasing pinniped abundance, however, there is currently no data regarding the actual frequency of depredation events.

Although it is straightforward to focus our attention on sea lions due to their gregarious nature and presence at highly visible and accessible haul out sites, we often overlook the more elusive harbor seals, which are present within the CR year round. Their numbers have also increased and adult harbor seals (many of which weigh upwards of 100 kg) are certainly capable of capturing and consuming adult salmon. In addition to causing direct mortality through predation, NMFS has been recording evidence of missed capture attempts by harbor seals (i.e. tooth and claw marks) at Lower Granite Dam since the early 1990s (Harmon et al. 1990). Although the incidence of tooth and claw marks has increased since the first observations, we have little empirical information about how these injuries affect survival of adult salmon (Naughton et al. 2011).

Based on our findings, it appears that recovering Interior CR spring-run Chinook salmon may be challenging given the number of pinnipeds currently residing in or transiently foraging within the CR. The conditions within the CR are similar to the southern Gulf of St. Lawrence, Canada where Swain and Benoit (2015) claimed that a fifteen fold increase in grey seals (*Halichoerus grypus*), created a predation driven Allee effect (i.e. continued population decline below a given threshold; Gascoigne and Lipcius 2004) on populations of large demersal fish that they will not recover from. The authors cite natural mortality of >40 - 50% for older age classes of Atlantic cod (*Gadus morhua*) as the principle cause for their continued decline despite negligible harvest. In our study we identified non-harvest related mortality of adult salmon ranging from 20 - 44 % annually. Given that average returns of wild spawners were 4 450 for the UCR and 33 133 for the SR from 2010-2015, our observed high-end mortality does not appear to be sustainable very far into the future (ODFW and WDFW 2016). Under an authorization pursuant to section 120 of the MMPA, the states of Oregon, Washington, and Idaho have been removing certain predatory pinnipeds in the vicinity of Bonneville Dam since 2008 (NMFS 2008; Tidwell et al. 2017). As the impact of pinniped predation on at-risk salmonids in the CR has expanded, Congress has proposed legislation to amend section 120 of the MMPA (e.g., HR 2083, S 1702, S 3119, and S 3315) to help address this threat to salmonid recovery further.

Finally, we observed that survival was lowest overall for fish tagged earlier in the run. Keefer et al. (2004) demonstrated a consistent order of return to Bonneville Dam by subpopulation for fish that had been injected with PIT-tags as juveniles. If there is also structure in the order of return to the estuary, this temporal trend in survival implies early returning subpopulations consistently experience lower survival compared to later returning subpopulations. Postponing harvest until later in the season may serve to protect early returning subpopulations from selectively experiencing the combined pressure of both predators and fishers as this would ensure a generous mix of subpopulations are within the river during harvest events. Opportunistic depredation of caught fish from fishing gear would also be reduced if peak predator presence and harvest were offset.

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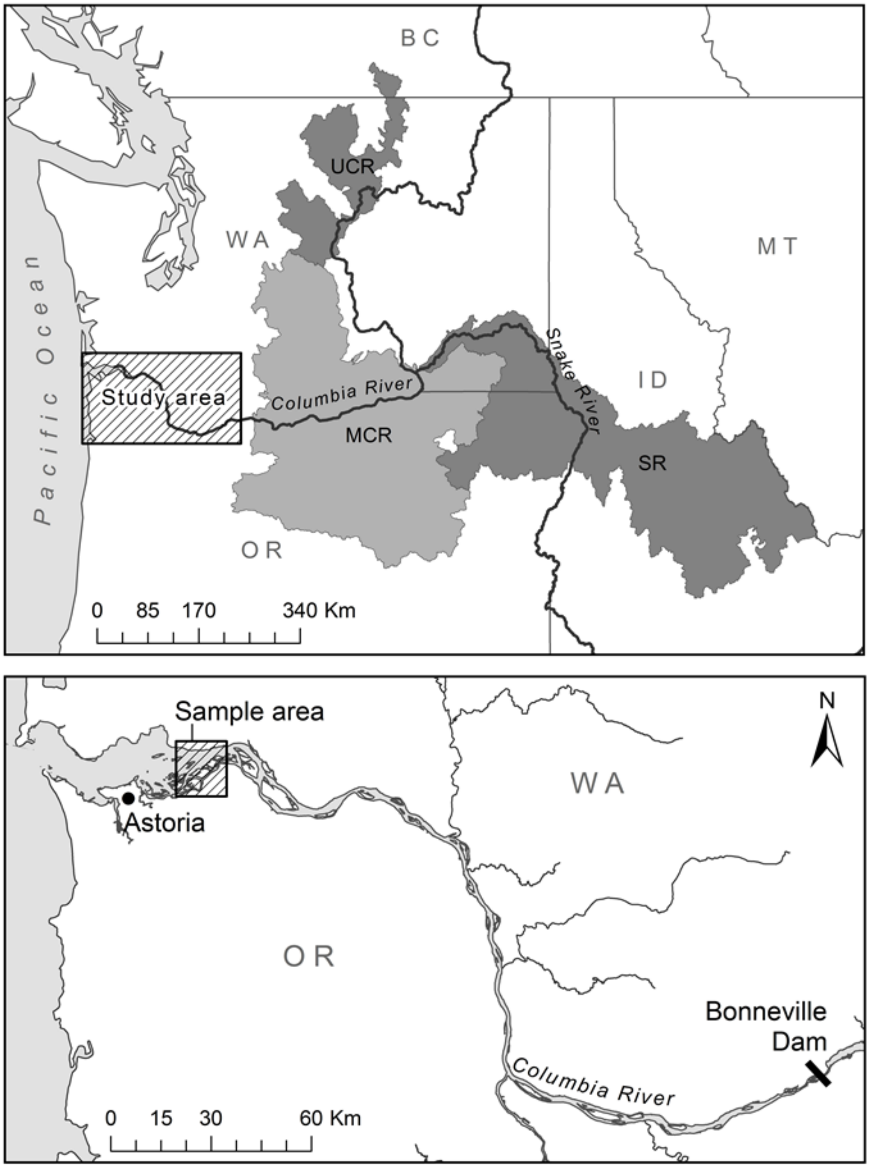

Map by Tyler Nodine, Ocean Associates, Inc., Seattle WA.

Fig. 1. Map of Pacific Northwest United States (top) shows study area below Bonneville Dam and spawning habitat for spring Chinook salmon (*Oncorhynchus tshawytscha*) populations of interest (UCR=Upper Columbia, MCR=Middle Columbia, and SR= Snake River). Bottom map shows sampling area near River km 44, Astoria Oregon (location of East Mooring Basin sea lion haul out site), and Bonneville Dam (River km 234).

Fig. 2. The sequence of handling and tagging that study fish were subjected to includes the exchange of Chinook salmon (*Oncorhynchus tshawytscha*) in tubes between the sampling and tagging vessel (a), study fish swimming of their own accord into a custom restraint device (b), study fish being injected with Passive Integrated Transponder tags (c), and study fish being released back into the river to resume migration (d).

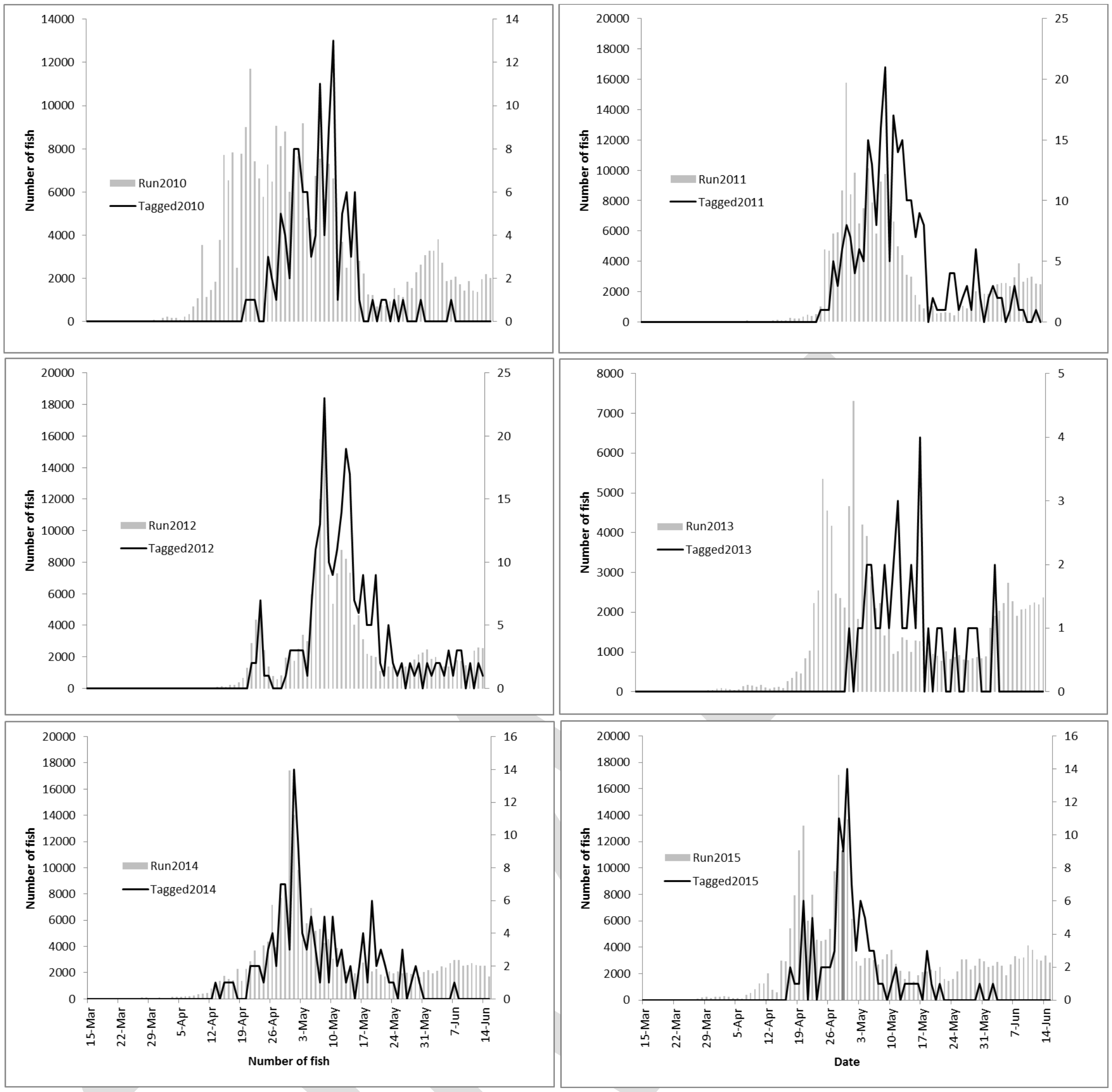

Fig. 3. The date of arrival at Bonneville Dam each year for our study fish (Tagged2010-2015) compared to the date of arrival at Bonneville Dam for the spring Chinook salmon (*Oncorhynchus tshawytscha*) run at large (Run2010-2015).

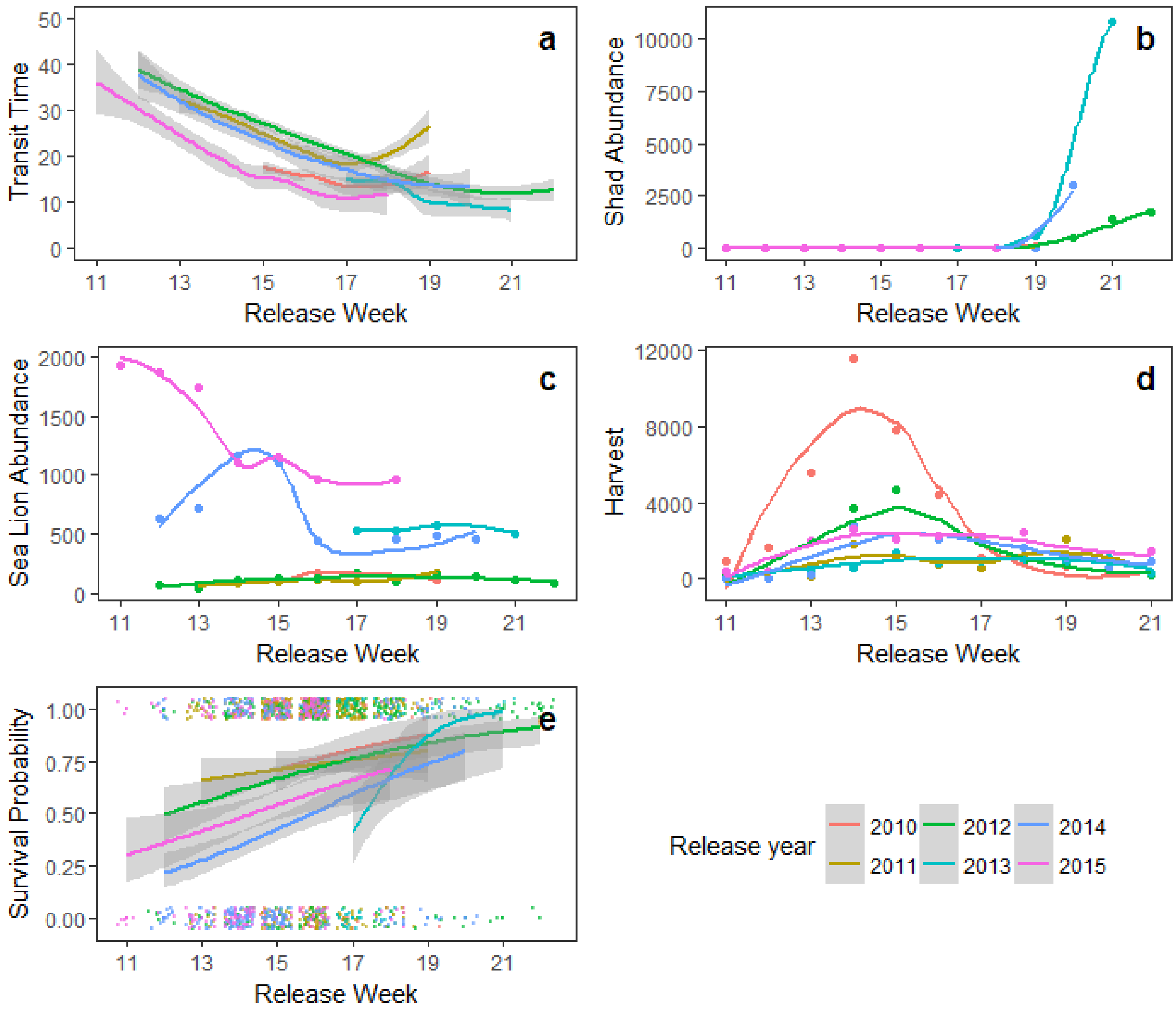

Fig. 4. Observed relationship between release week and (a) transit time of surviving fish from release location to Bonneville Dam, (b) log American Shad (*Alosa sapidissima*) abundance, (c) California Sea Lion (*Zalophus californianus*) abundance, (d) harvest, and (e) Adult salmon survival probability. Lines in a, b, c, and d were fit with loess smooths, while the line in e is the fit of a logistic regression with release week as the only predictor. Grey shading represents 95% confidence intervals.

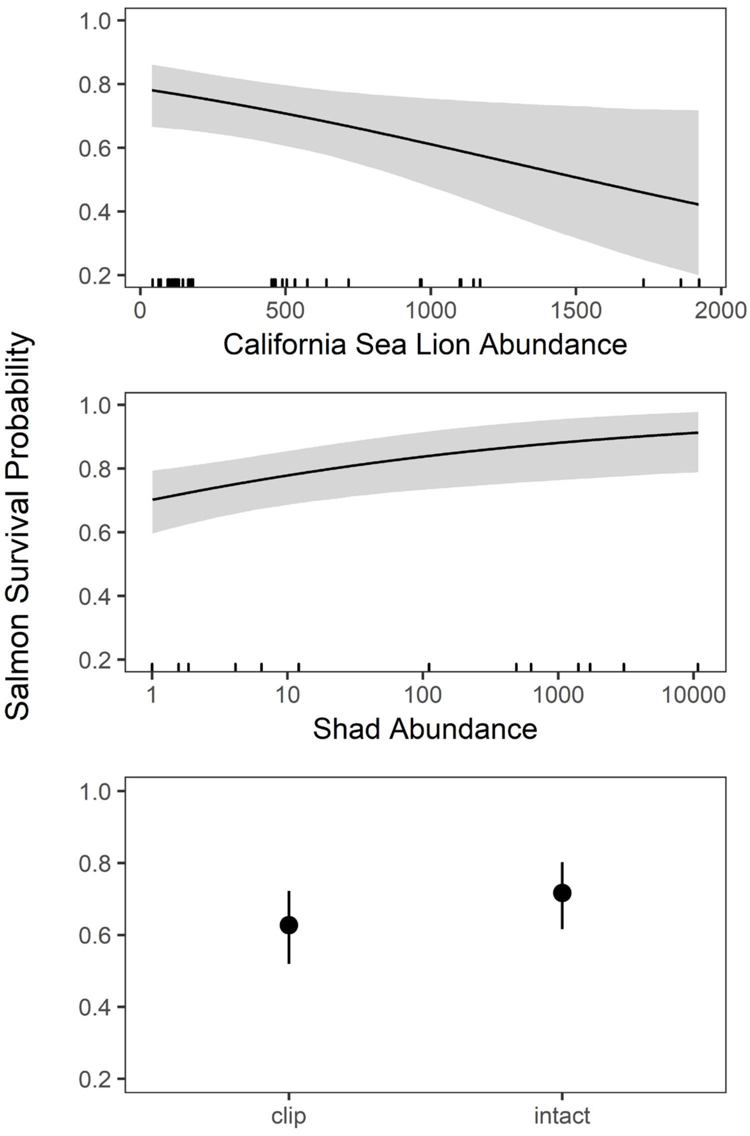

Fig. 5. Model response curves illustrating the relationship between salmon survival and (top) California Sea Lion (*Zalophus californianus*), abundance, (middle) American Shad (*Alosa sapidissima*) abundance, and (bottom) clip status. The y-axis for each graph represents survival probability and the x-axis is the range of observed values for each covariate. Vertical lines perpendicular to the x-axis represent covariate values observed during our study and do not reflect the frequency of occurrence.

Table 1. Sample size and release dates for PIT-tagged adult Chinook salmon (*Oncorhynchus tshawytscha*) destined for tributaries above Bonneville Dam.

Release	Release Week												Total
year	11	12	13	14	15	16	17	18	19	20	21	22	released
2010	0	0	0	0	66	62	34	0	7	0	0	0	169
2011	0	0	26	19	66	121	76	43	10	0	0	0	361
2012	0	9	11	51	51	87	51	40	10	13	12	15	350
2013	0	0	0	0	0	0	29	17	5	0	5	0	56
2014	0	16	19	100	72	33	0	20	18	10	0	0	288
2015	7	6	28	55	29	59	0	16	0	0	0	0	200

Table 2. Covariates related to potential survival mechanisms that were considered for logistic regression modelling.

Covariate	**Hypothesized relationship to adult Chinook salmon survival**
Year	Annual variation of environmental and biological covariates will influence survival
Release week	Fish tagged within the same week will have similar survival probabilities due to shared lineage and/or prior experience
Length	Smaller fish are preferred by pinnipeds and/or larger fish are more capable of avoiding and/or escaping predators than their smaller conspecifics
Clipped adipose fin	Adipose clipped fish will have lower survival due to harvest
Shad abundance[a]	Serves as alternative prey item for pinniped predators
Sea lion abundance[b]	Survival will decrease as the number of sea lions hauled out near Astoria, OR increases
Shad * Sea lion interaction	Survival will increase relative to shad abundance only when sea lions are present

[a] Daily counts of adult shad over Bonneville Dam were adjusted back (i.e. earlier) two weeks in time to estimate time of estuary entrance based on Moser and Ross 1994.

[b] Index of abundance based on the weekly estimated number of sea lions hauled out at the East Mooring Basin, Astoria, OR. Data source: Matthew Tennis, Oregon Department of Fish and Wildlife, Astoria, Oregon.

Table 3. Model selection results for the ten candidate models.

Candidate fixed effects	d.f.	logLik	AIC	ΔAIC	weight
Clip, CSL, logShad	6	-863.32	1738.71	0.00	0.38
Clip, CSL, logShad, Length	7	-862.44	1738.96	0.26	0.33
Clip, CSL * logShad	7	-863.32	1740.72	2.01	0.14
Clip, CSL * logShad, Length	8	-862.44	1740.98	2.27	0.12
Clip, CSL	5	-868.15	1746.34	7.63	0.01
Clip, logShad	5	-868.15	1746.34	7.64	0.01
Clip, CSL, Length	6	-867.23	1746.52	7.81	0.01
Clip, logShad, Length	6	-867.39	1746.84	8.14	0.01
Clip	4	-874.47	1756.96	18.26	<0.01
Clip, Length	5	-873.66	1759.37	18.66	<0.01

Note: The following *fixed-effects* covariates were tested against fish survival: Length (=Adult salmon fork length), Clip (= no adipose fin), CSL (= estimate of sea lion abundance during release week), logShad (= log estimate of shad abundance during release week). We also included an interaction between CSL and logShad. A *random effect* for release week nested within year was included in each of the models tested.

Table 4. Final generalized linear mixed model fit to the survival data (n=1473 individuals, n=41 release weeks). Intercept = model intercept, Clip = adipose fin clip status, CSL = California Sea Lion abundance at East Mooring Basin, logShad = log estimate of Shad abundance during release week, σ^2 = variance, ρ = covariance autocorrelation, deviance = model deviance.

Parameter	**Mean**	**Std Dev**	**2.5%**	**50%**	**97.5%**
Intercept	0.94	0.24	0.47	0.94	1.4
Clip	-0.42	0.14	-0.70	-0.41	-0.14
CSL	-0.40	0.17	-0.71	-0.41	-0.04
logShad	0.27	0.11	0.07	0.27	0.48
σ^2	0.53	0.16	0.29	0.51	0.91
ρ	0.51	0.21	0.13	0.53	0.87
deviance	1697.71	8.61	1682.48	1697.07	1715.78

Table 5. Annual estimated number of spring run Chinook salmon lost to sources other than harvest between the Columbia River Estuary and Bonneville Dam. Credible intervals were estimated based on 100 000 random draws from the model parameter posteriors. Non-harvest mortality was the mean number of mortalities not attributed to harvest divided by the estimated total number of fish in the estuary in each year. Numbers are in thousands.

Year	**Mean**	**Std Dev**	**2.5%**	**50%**	**97.5%**	**Non-harvest mortality**
2010	77.56	21.72	43.36	74.71	127.43	0.20
2011	59.48	16.71	33.18	57.27	97.83	0.22
2012	51.75	14.39	29.08	49.86	84.80	0.20
2013	35.21	9.11	20.60	34.11	56.14	0.22
2014	98.47	26.05	57.30	95.16	158.53	0.29
2015	224.45	107.98	85.65	201.25	495.21	0.44

Table S1. Average daily survival for tagged adult Chinook salmon (*Oncorhynchus tshawytscha*) by month tagged along with the average temperature and the number of tagging dates survival was equal to 100%.

Month	**Fish tagged (N)**	**Tagging dates (N)**	**Days with 100% Survival (N)**	**Average daily survival (range)**	**Average river temperature at tagging ^{0}C**
March	77	12	2	44% (0 - 100%)	8.2
April	1137	67	1	60% (0 - 100%)	9.8
May	210	37	11	75% (0 - 100%)	12.4

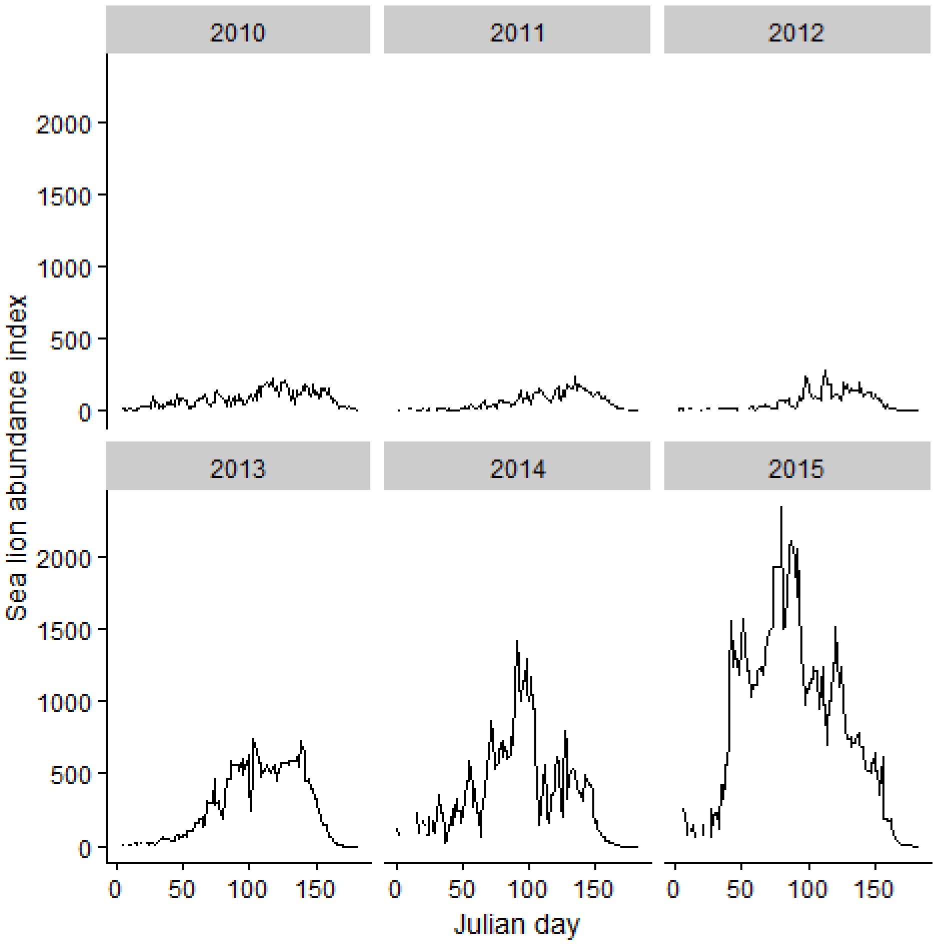

Fig. S1. Sea Lion (*Zalophus* and *Eumetopias*) abundance at the East Mooring Basin, Astoria, Oregon on each Julian day throughout the survey period.

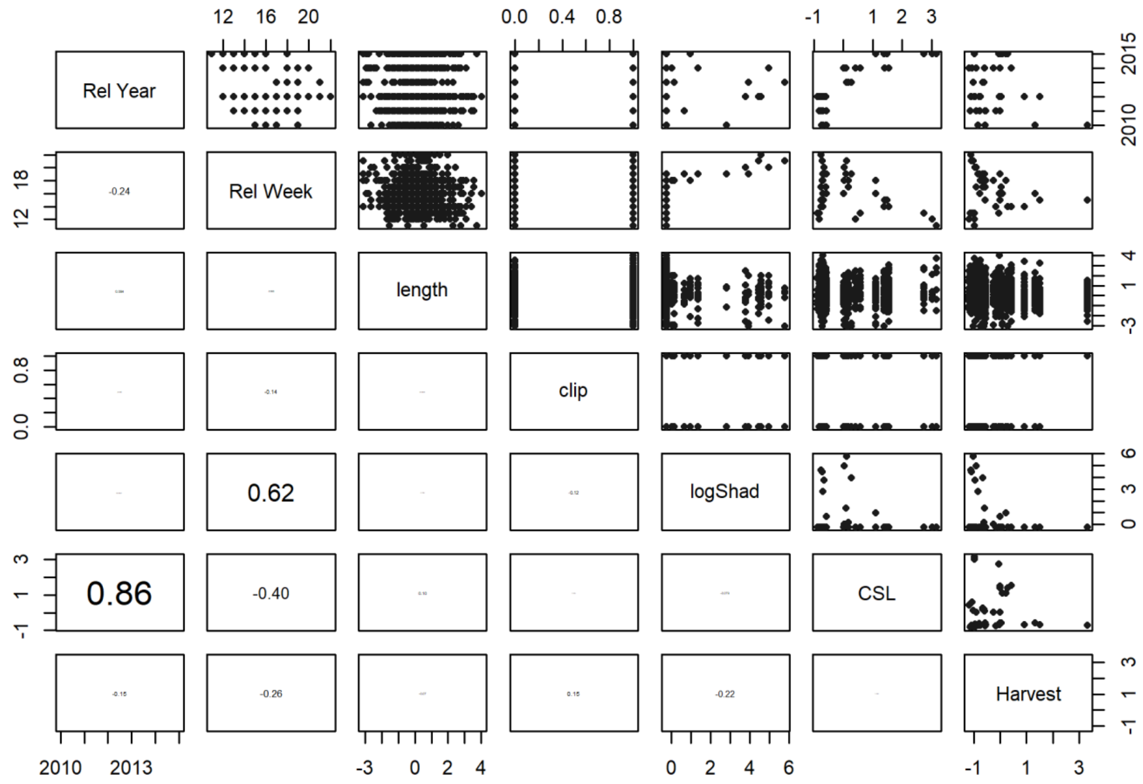

Fig. S2. Collinearity plot between all standardized covariates considered in the generalized Linear Mixed-Effects Model. The values in the lower left portion of the plot are Pearson correlation coefficients and the font size is proportional to the correlation. Rel Year = release year, Rel Week = release week, Length = fork length, Clip = adipose fin clip status, logShad = log of American shad (*Alosa sapidissima*) abundance, CSL = California sea lion (*Zalophus* and *Eumetopias*) abundance at the East Mooring Basin, Astoria, Oregon, and Harvest = commercial salmon harvest.